PROC. ENTOMOL. SOC. WASH.
105(4), 2003, pp. 847–858

BIODIVERSITY AND ECOLOGY OF MYCOPHAGOUS DIPTERA IN NORTHEASTERN OHIO

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Abstract.—For this study, 134 species from 30 families of Basidiomycete fungi and 19 species from 11 families of Ascomycete fungi were collected from different sites in northeastern Ohio. Adult flies were reared from 87 separate fungal collections (basidiocarps or ascocarps = "mushrooms"). During this study, mycophagous species from a number of families were found (Tipulidae, Mycetophilidae, Sciaridae, Cecidomyiidae, Phoridae, Platypezidae, Chloropidae, Drosophilidae); the two most common fly species were *Drosophila falleni* Wheeler and *Leucophenga varia* Walker, both Drosophilidae. Less commonly found were *Drosophila tripunctata* Loew, *Drosophila putrida* Sturtevant, and *Mycodrosophila claytonae* Wheeler and Takada. Frequently, several species of Drosophilidae were found cohabiting the same mushroom. Unless factors are in operation to prevent competition (niche partitioning, predation, parasitism), mycophagous Diptera may pose a challenge to the Competitive Exclusion Principle. Preliminary evidence suggests parasitism and predation by other species of arthropods may play a role in reducing competition.

Key Words: Competitive Exclusion Principle, fungi-feeding flies, mushrooms

The sporophores of macrofungi (i.e., mushrooms of Basidiomycetes and Ascomycetes) are analogous to vascular plants in a number of ways: they are immobile, frequently contain chemical toxins, have few physical defenses, and have members that may be ephemeral or perennial in longevity (Hanski 1989). Fungi are found in virtually every ecological niche, and the sporophores of many groups of macrofungi serve as hosts of mycophagous Diptera. Despite the frequency and diversity of Diptera that inhabit mushrooms, few studies have been concerned with mycophagous species. Most such ecological studies were conducted several decades ago (Buxton 1960, Pielou 1966, Pielou and Mathewman 1966, Pielou and Verma 1968, Valley et al. 1969, Papp 1972, Shorrocks and Wood 1973) and often gave only anecdotal accounts of adult flies occurring on mushrooms (Patterson 1943, Valley et al. 1969, Graves and Graves 1985), not verifying true mycophagy. Still other studies have included flies as mycophages, where only one or two adults emerged from fungal material (Buxton 1960, Valley et al. 1969, Hackman and Meinander 1979, Graves and Graves 1985, Yakolev 1993), or had emerged solely from decaying mushrooms (thus, possibly only scavenging) (Frouz and Makarova 2001) and therefore did not establish a strong ecological association (i.e., food substrate, site of overwintering, etc.) with fungal sporocarps. Still other studies have focused on the evolution of tolerance of the amanitin toxin (present throughout the Basidiomycete genus *Amanita* Persoon) tolerance (Jaenike et al. 1983, Jaenike 1985) or mechanisms for aggregation of adult flies on mushrooms (Jaenike et al. 1992).

Overlooked by nearly all studies has been the ecology of mushroom-feeding species, and little is known about larval stages, feeding preferences, seasonality, or geographic range for numerous species (Buxton 1960; Graves and Graves 1985; Bunyard and Foote 1990a, b). The larval stages of many of the rarer species of mycophagous flies have never been described. Most mycophagous flies are probably generalists and not specific to any species of fungus, as fungal hosts are considered too patchy and/or ephemeral, or are scavengers, feeding on all sorts of decaying organic material (Jaenike 1978a, b). Oligophagous and specialist species are uncommon in nature and in the literature; many of the records reporting monophagy are likely artifacts of insufficient sampling (Hanski 1989). It has been postulated that mycophagous Diptera probably arose from ancestral detritivores (Bruns 1984). One of the largest groups of mycophagous Diptera, the family Drosophilidae, is considered to have evolved mycophagy more than once from a common ancestor that was a detritivore or fed on saprophytic yeasts (Courtney et al. 1990).

For this study I attempted to determine: a) the families of Diptera that are truly mycophagous, b) the existence of associations among families of Diptera with families of Basidiomycete host fungi, c) seasonality among mycophagous families of Diptera, and d) evidence of seasonality within a common mycophagous family, the Drosophilidae.

Materials and Methods

Sites were selected to obtain a diversity of mushroom species, as well as biotic and abiotic conditions, and consisted of mature forest, mixed mesophytic forest, urban forest, and urban residential zones in northeastern Ohio (Cuyahoga, Geauga, and Portage counties). Two of the study sites have been described previously: Towner's Woods near Kent, Ohio (Portage Co.) (Bunyard and Foote 1990a) and The West Woods, near Newbury, Ohio (Geauga Co.) (Bunyard, in press).

Fungi were collected throughout the growing season from March to November, 2001. Many fungal species were collected more than once and/or on different dates or sites. Fungal material was placed in paper bags to prevent larvae of one sporophore from entering another sporophore. Different species were kept in separate bags; conspecifics from different sites also were kept separately. Fungal specimens were identified using keys in Lincoff 1984, Arora 1986, Phillips 1991, Smith and Weber 1996, Bessette et al. 1997. To avoid incidental occurrences of Diptera with the fungi (for example, resting or hiding in crevices) only adults which actually emerged from larvae occurring within the fungus were counted.

For rearing adult flies from fungal hosts, special rearing chambers were constructed as previously described (Bunyard and Foote 1990a) and consisted of the bottom of a petri dish (10 × 100 mm) to which had been added moistened vermiculite. The upper portion of the rearing chamber consisted of rigid clear plastic tubing (90 mm diameter) cut to various lengths. To the top end of each tube was glued a fine polyester mesh material. Fungal sporocarps were placed on the vermiculite substrate, and the upper portion of the chamber placed securely over the fungus, into the petri plate. The rearing chambers allowed the fungal specimens to remain in a somewhat natural condition. It was necessary to moisten the vermiculite substrate periodically to prevent desiccation of fungal material. As the sporocarps decayed, the substrate absorbed any excess moisture produced.

Following emergence, adult Diptera were kept alive for at least 24 hr to allow for exoskeleton hardening (to facilitate identification) and then killed in alcohol. Adult flies were dried and pinned for identification. Preserved specimens are in the Kent State University collection of Diptera.

Results

During this study 134 species from 30 families of Basidiomycete fungi and 19 species from 11 families of Ascomycete fungi were collected from different sites in northeastern Ohio. Adult flies were reared from 87 separate fungal collections (Table 1). A few fungal species seemed to host only a single fly species per mushroom, but most were found to support more than one species of Diptera (Table 2). Five families of Diptera that include known or suspected mycophagous species (Tipulidae, Phoridae, Platypezidae, Chloropidae, Drosophilidae) were reared from fresh mushroom collections (Table 2), confirming mycophagy (as opposed to scavengening rotting material). Additionally, members of the Mycetophilidae, Sciaridae, and Cecidomyiidae also were seen (data not shown). Five other dipteran families that were reared from fungi (Psychodidae, Ceratopogonidae, Stratiomyiidae, Anthomyiidae, Sarcophagidae) likely are larval predators or scavengers occurring only in decaying mushrooms (Table 2). In some cases a single member of a dipteran family emerged from fungal material but was not counted, as it was unclear if any strong ecological association with fungi existed.

Discussion

All Diptera reared in this study emerged only from Basidiomycete species (Table 1). No evidence for monophagy was seen by any of the dipteran taxa. In general, the larger the sporocarps, the greater the number of individuals, as well as diversity, of Diptera utilizing the mushroom host were seen, supporting previous studies (Bruns 1984, Hanski 1989). Previous demonstration of seasonality of mycophagous Diptera has been considered a function of seasonality of mushroom hosts (Hanski 1989) and was demonstrated here (Fig. 1). The highest number of emergences for all mycophagous taxa was seen in spring and fall; this correlated to the highest numbers of mushroom fruitings (Fig. 1).

More rearings of Drosophilidae were recorded than those of any other dipteran family (Fig. 1). The highest number of emergences for drosophilid species was seen in spring and fall. Thus, seasonality of mycophagous Drosophilidae likely is due to seasonality of hosts. Most species of Drosophilidae are considered yeast-feeders (Patterson 1943), with the food material serving as a culture medium for the yeast. It is thought that all extant species of this family came from a common ancestor that was detritivorous (Courtney et al. 1990) and became selective for rotting substrates supportive of yeast growth, especially fruits. Phylogenetic evidence suggests that mycophagy has arisen more than once within the family (Courtney et al. 1990). Today, most species of drosophilids feed on decaying fruit material, some are scavengers, and a few feed on fungi. All the species reared in this study (*Drosophila falleni* Wheeler, *D. putrida* Sturtevant, *D. tripunctata* Loew, *Mycodrosophila claytonae* Wheeler and Takada, *Leucophenga varia* Walker) are known to be mycophagous. During this study, the two most commonly reared species overall were *D. falleni* and *L. varia* (Fig. 2). These two species commonly coinhabited basidiocarps, occasionally with three other less common drosophilids: *D. tripunctata*, *D. putrida*, and/or *M. claytonae*. These findings support those of previous studies (Grimaldi and Jaenike 1984). Some drosophilid species have been shown to dominate (*D. tripunctata*) when competing with other species (*D. falleni* and *D. putrida*) (Worthen 1989), although this clearly was not seen here. Likewise, *Leucophenga* species may dominate in smaller species of mushrooms (Worthen et al. 1998). Several species of mycophagous species of Drosophilidae that were reared from fungi previously (Bunyard and Foote 1990a) were not obtained in this study, including *D. duncani* Sturtevant, *D. guttifera* Walker, *D. testacea* von Roser, and *M. dimidiata* Loew. Little is known about the life history of *D. duncani*. Likewise, *D. gutti-*

Table 1. Species of macrofungi, serving as hosts for mycophagous Diptera, arranged alphabetically by fungal family.

Family	Species	Diptera Species	Diptera Family
?	agaric sp.?	*Drosophila falleni*	Drosophilidae
Agaricaceae	*Agaricus arvensis* Schaeffer	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
	Agaricus augustus Fries	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Agaricus bitorquis Quelet	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
			Phoridae
	Agaricus campestris Linnaeus	*Leucophenga varia*	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
	Agaricus sp.	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
Amanitaceae	*Amanita flavorubescens* Atkinson	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Amanita muscaria Persoon	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
	Amanita rubescens Persoon	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
		Leucophenga varia	Drosophilidae
Bolbitiaceae	*Agrocybe praecox* Persoon	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
Boletaceae	*Boletus bicolor* Peck	*Drosophila falleni*	Drosophilidae
		Drosophila putrida	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Boletus edulis Bulliard	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Sarcophagidae
	Boletus sp.	sp. #1	Anthomyiidae
		Drosophila falleni	Drosophilidae
Cortinariaceae	*Cortinarius* sp.	*Drosophila falleni*	Drosophilidae
			Phoridae
	Galerina autumnalis Peck		Phoridae
Coprinaceae	*Psathyrella delineata* Peck	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
		Leucophenga varia	Drosophilidae
Hygrophoraceae	*Hygrophorus marginatus* Peck	*Leucophenga varia*	Drosophilidae
Pluteaceae	*Pluteus cervinus* Schaeffer	*Drosophila falleni*	Drosophilidae
			Phoridae
		Platypeza sp.	Platypezidae
			Sarcophagidae
Polyporaceae	*Bondarzewia berkeleyi* Fries	*Drosophila falleni*	Drosophilidae
		Mycodrosophila claytonae	Drosophilidae
			Phoridae
	Grifola frondosa Fries	*Drosophila falleni*	Drosophilidae

Table 1. Continued.

Family	Species	Diptera Species	Diptera Family
	Laetiporus sulfureus Fries	*Tricimba lineella*	Chloropidae
		Drosophila falleni	Drosophilidae
	Polyporus arcularius Bataille	*Drosophila falleni*	Drosophilidae
	Tyromyces chioneus Fries	*Limonia rara*	Tipulidae
Russulaceae	*Russula aeruginea* Lindblad	*Drosophila falleni*	Drosophilidae
	Russula brevipes Peck	*Drosophila putrida*	Drosophilidae
			Phoridae
		Ptecticus sp.	Stratiomyidae
		Limonia triocellata	Tipulidae
	Russula emetica Schaeffer	*Drosophila falleni*	Drosophilidae
		Ptecticus sp.	Stratiomyidae
	Russula mariae Peck	*Drosophila putrida*	Drosophilidae
		Leucophenga varia	Drosophilidae
	Russula ochroleucoides Kauffman	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Russula sp.	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
Strophariaceae	*Hypholoma fasciculare* Hudson	*Drosophila falleni*	Drosophilidae
	Pholiota malicola Kauffman	*Leucophenga varia*	Drosophilidae
	Pholiota sp.	*Limonia triocellata*	Tipulidae
	Pholiota sp.		Ceratopogonidae
		Drosophila falleni	Drosophilidae
			Psychodidae
Tricholomataceae	*Collybia acervata* Fries	*Drosophila falleni*	Drosophilidae
		Leucophenga sp.	Drosophilidae
	Mycena leaiana Berkeley	*Drosophila falleni*	Drosophilidae
		Leucophenga sp.	Drosophilidae
	Omphalotus olearius Schweinitz	*Drosophila putrida*	Drosophilidae
	Pleurotus dryinus Persoon		Phoridae
	Pleurotus ostreatus Jacquin	*Drosophila falleni*	Drosophilidae
		Drosophila tripunctata	Drosophilidae
		Leucophenga varia	Drosophilidae
		Mycodrosophila claytonae	Drosophilidae
			Phoridae
		Limonia triocellata	Tipulidae
	Tricholomopsis platyphylla Persoon	*Drosophila falleni*	Drosophilidae
		Leucophenga varia	Drosophilidae
			Phoridae
	Xerula furfuracea Peck	sp. #1	Anthomyiidae
		sp. #2	Anthomyiidae
		Drosophila falleni	Drosophilidae
		Limonia triocellata	Tipulidae

fera apparently is a rare mycophagous species known from only a few records (Patterson 1943). Bunyard and Foote (1990a) provided the only record for this species in Ohio. In a study of its life history, ovipositional preferences, and larval feeding habits it was found to be polyphagous for fruits and other vegetation, but with a strong preference for mushroom tissue (Bunyard and Foote 1990b).

Phoridae, a family of small flies, also is described as one of the most common inhabitants of fungal sporocarps (Hackman and Meinander 1979). Larvae are frequent-

Table 2. Species of mycophagous Diptera, arranged phylogenetically by family, reared from mushroom sporophores.

Family	Species	Fungus Family	Fungus Species
Tipulidae	*Limonia rara* Osten Sacken	Polyporaceae	*Tyromyces chioneus*
	Limonia triocellata Osten Sacken	Russulaceae	*Russula brevipes*
	Limonia triocellata Osten Sacken	Strophariaceae	*Pholiota* sp.
	Limonia triocellata Osten Sacken	Tricholomataceae	*Pleurotus ostreatus*
	Limonia triocellata Osten Sacken	Tricholomataceae	*Xerula furfuracea*
Psychodidae	Sp.?	Strophariaceae	*Pholiota* sp.
Ceratopogonidae	Sp.?	Strophariaceae	*Pholiota* sp.
Stratiomyidae	*Ptecticus* sp.	Russulaceae	*Russula brevipes*
	Ptecticus sp.	Russulaceae	*Russula emetica*
Phoridae		Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus bitorquis*
		Agaricaceae	*Agaricus campestris*
		Amanitaceae	*Amanita flavorubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Cortinariaceae	*Cortinarius* sp.
		Cortinariaceae	*Galerina autumnalis*
		Pluteaceae	*Pluteus cervinus*
		Pluteaceae	*Pluteus cervinus*
		Polyporaceae	*Bondarzewia berkeleyi*
		Polyporaceae	*Bondarzewia berkeleyi*
		Russulaceae	*Russula brevipes*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Tricholomataceae	*Pleurotus dryinus*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
Platypezidae	*Platypeza* sp.	Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus campestris*
		Pluteaceae	*Pluteus cervinus*
Chloropidae	*Tricimba lineella* Fallén	Agaricaceae	*Agaricus arvensis*
	Tricimba lineella Fallén	Coprinaceae	*Psathyrella delineata*
		Polyporaceae	*Laetiporus sulfureus*
Drosophilidae	*Drosophila falleni* Wheeler	?	Agaric sp.?
		Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus bitorquis*
		Agaricaceae	*Agaricus* sp.
		Amanitaceae	*Amanita flavorubescens*
		Amanitaceae	*Amanita muscaria*
		Amanitaceae	*Amanita rubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Boletaceae	*Boletus edulis*
		Boletaceae	*Boletus* sp.
		Cortinariaceae	*Cortinarius* sp.
		Coprinaceae	*Psathyrella delineata*
		Pluteaceae	*Pluteus cervinus*
		Polyporaceae	*Bondarzewia berkeleyi*
		Polyporaceae	*Grifola frondosa*
		Polyporaceae	*Laetiporus sulfureus*
		Polyporaceae	*Polyporus arcularius*
		Russulaceae	*Russula aeruginea*

Table 2. Continued.

Family	Species	Fungus Family	Fungus Species
		Russulaceae	*Russula emetica*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Strophariaceae	*Hypholoma fasciculare*
		Strophariaceae	*Pholiota* sp. 1
		Tricholomataceae	*Collybia acervata*
		Tricholomataceae	*Mycena leaiana*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
		Tricholomataceae	*Xerula furfuracea*
Drosophilidae	*Drosophila putrida* Sturtevant	Agaricaceae	*Agaricus bitorquis*
		Amanitaceae	*Amanita muscaria*
		Amanitaceae	*Amanita rubescens*
		Boletaceae	*Boletus bicolor*
		Russulaceae	*Russula brevipes*
		Russulaceae	*Russula mariae*
		Tricholomataceae	*Omphalotus olearius*
Drosophilidae	*Drosophila tripunctata* Loew	Tricholomataceae	*Pleurotus ostreatus*
Drosophilidae	*Leucophenga varia* Walker	Agaricaceae	*Agaricus augustus*
		Agaricaceae	*Agaricus campestris*
		Agaricaceae	*Agaricus* sp.
		Amanitaceae	*Amanita flavorubescens*
		Amanitaceae	*Amanita rubescens*
		Bolbitiaceae	*Agrocybe praecox*
		Boletaceae	*Boletus bicolor*
		Boletaceae	*Boletus edulis*
		Coprinaceae	*Psathyrella delineata*
		Hygrophoraceae	*Hygrophorus marginatus*
		Russulaceae	*Russula mariae*
		Russulaceae	*Russula ochroleuca*
		Russulaceae	*Russula* sp.
		Strophariaceae	*Pholiota malicola*
		Tricholomataceae	*Pleurotus ostreatus*
		Tricholomataceae	*Tricholomopsis platyphylla*
Drosophilidae	*Leucophenga* sp.	Tricholomataceae	*Collybia acervata*
		Tricholomataceae	*Mycena leaiana*
Drosophilidae	*Mycodrosophila claytonae* Wheeler and Takada	Polyporaceae	*Bondarzewia berkeleyi*
		Tricholomataceae	*Pleurotus ostreatus*
Anthomyiidae	Sp. #1	Boletaceae	*Boletus* sp.
	Sp. #1	Tricholomataceae	*Xerula furfuracea*
	Sp. #2	Tricholomataceae	*Xerula furfuracea*
Sarcophagidae	Sp.?	Agaricaceae	*Agaricus arvensis*
		Agaricaceae	*Agaricus campestris*
		Boletaceae	*Boletus edulis*
		Pluteaceae	*Pluteus cervinus*

ly found in decaying vegetation and fungi; some species (especially of the genus *Megaselia* Rondani) are serious pests of commercial mushroom farms; a few species are known to be parasitic on other insects. During this study, phorid flies emerged from more sporocarp collections than any other group except the Drosophilidae (Fig. 1).

Two species of Tipulidae, *Limonia rara* Osten Sacken and *L. triocellata* Osten

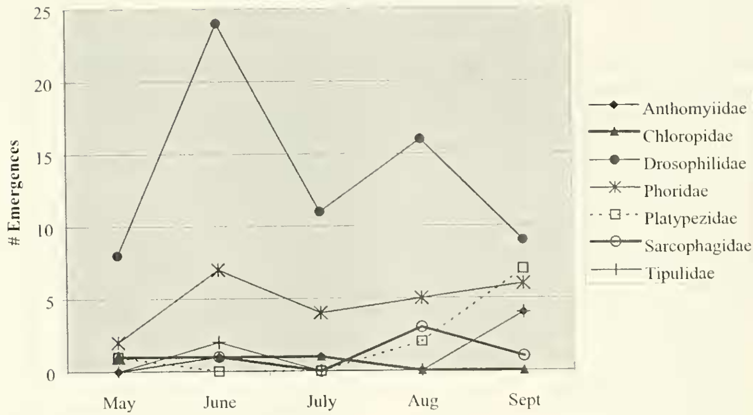

Fig. 1. Emergence numbers by month for families of Diptera.

Sacken, were reared in this study (Table 2). Most larvae of Tipulidae feed in decaying plant materials and frequently are aquatic or semi-aquatic, although several species are terrestrial. Tipulids have been reared from fungi previously (Alexander 1920, Bruns 1984). *Limonia triocellata* is a known consumer of decaying organic material (B. Foote, personal communication) and has been reared from senescent as well as fresh mushrooms (Bruns 1984). However, no information is available for the feeding substrate of larval *L. rara.* Several adults of *L. rara* were reared from sporocarps of the soft moist bracket fungus *Tyromyces chioneus* Fries. As the infested sporocarps

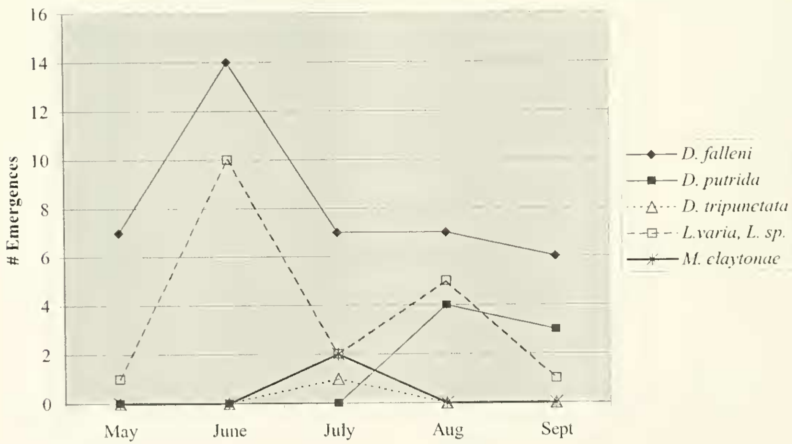

Fig. 2. Emergence numbers by month for species of Drosophilidae.

were newly emerged, this may indicate a strictly mycophagous (as opposed to scavenging on decaying fungal or other organic material) feeding habit for this species. No species of Tipulidae currently are considered to be strictly mycophagous.

Tricimba lineella Fallèn (Chloropidae) was reared on a number of occasions (Table 2). *Tricimba lineella* previously has been recorded from rotting plant material (Grimaldi and Jaenike 1983) and from macrofungi (Bunyard and Foote 1990a). One other species (*Gaurax atripalpus* Sabrosky) has been recorded from fungi, probably overwintering in polyporaceous species (Valley et al. 1969, Bunyard and Foote 1990a).

The family Platypezidae was reared from fresh sporocarps mostly towards the end of the growing season (Fig. 1). The association was especially significant between this family and the basidiomycete family Agaricaceae, as platypezids were reared almost exclusively from species of *Agaricus* (Table 2). Species of *Agaricus* produce some of the largest sporocarps and would seem an ideal host, but they seem to be rarely utilized by other mycophagous Diptera (Buxton 1960, Hackman and Meinander 1979). Members of the Platypezidae (the "flat-footed" or "smoke flies") comprise a small family (71 species in 18 genera in North America) of uncommon flies of wooded areas (Kessel 1987). Adult platypezids are noted by a fairly large head and characteristic flattened hind tarsi and tibiae. Although all platypezid species are thought to be mycophagous, the life cycles and larvae for many species remain unknown or have never been seen (Kessel 1987).

Unidentified adults from the families Anthomyiidae and Sarcophagidae were reared from a number of large, mostly decaying, Basidiomycete sporocarps (Fig. 1) suggesting scavenging behavior and not strict mycophagy. Both families are comprised of large bodied species that commonly are scavengers of decaying organic material.

Curiously, several species of mycophagous Diptera were conspicuously absent from this study. For example (besides those already mentioned above), *Leiomyza laevigata* Meigen (Asteiidae) is a rare species known from only a handful of studies (Sabrosky 1957, Papp 1972). Bunyard and Foote (1990a) confirmed its mycophagous habit.

Frequently, larvae of more than one family—often from several families—occupied the same sporocarp. Likewise, more than one species from a single family frequently emerged from the same sporocarp. Because fungal sporocarps are a limited and ephemeral food source, it would seem logical that inter- and intraspecific competition pressures should exist. The Competitive Exclusion Principle (Hardin 1960) states that two species cannot coexist in a single limiting resource. So, how can we explain so many closely related species occupying the same niche? Previously, a few studies have provided possible explanations as to how species of mycophagous Diptera avoid significant interspecies competition. In particular, most studies have focused on the commonly seen mycophagous species of Drosophilidae. Biotic pressures (predation, parasitism) may reduce competition and thus allow drosophilid species to cohabit (Worthen 1989, Worthen et al. 1995, Jaenike 1998). Predation by ants and beetles, and parasitism by nematodes were the focus. During this study, numerous predacious beetles frequently were seen feeding (presumably on fly larvae) on and within mushroom tissues, especially the larger Basidiomycete species that were associated with rearings of multiple species of drosophilids and other taxa. Adult parasitic Hymenoptera frequently emerged from the sporocarps. Presumably, parasitic wasps also could impinge upon the fly species to reduce their numbers, and thus lessen interspecific competition pressures.

Abiotic pressures also may reduce competition and allow different fly species to cohabit. Worthen and Haney (1999) found that when abiotic pressures (heat, desiccation) are strong, other dipterous species may dominate (e.g., *D. putrida* is more common in small mushrooms that are more subject to desiccation and was found to be more tolerant of chronic and acute bouts of drought or high temperatures). Our findings strongly support this; *D. putrida* was seen as a dominant species only in the months of August and September (Fig. 2).

Most of the attention of this paper—and the interrelationship between Diptera and fungal host—has been approached from the fly's point of view. It may be just as interesting to consider the host's (fungus) role in this symbiosis. Typical levels of mycophagy frequently resulted in the complete destruction of the sporocarp. One would think this to be detrimental to the host. If this is true, it is logical to expect the host to fight back (the "Red Queen" effect [Van Valen 1973]). Few studies have attempted to determine if any macrofungi are unsuitable to any groups of flies. Of course, by virtue of size alone, those fungi that form particularly small sporocarps will escape or have reduced mycophagy. Similarly, a few fungal species avoid damage by their physical makeup: many species of bracket fungi (mostly within the family Polyporaceae) have a hard, woody texture that is difficult for many arthropods to consume (Courtney et al. 1990). Basidiomycete and Ascomycete fungi produce a wide array of toxic metabolites, although the defensive properties of these have been poorly investigated. Insecticidal properties have been explored (Mier et al. 1996), although the authors carried out their study by feeding mushroom extracts to arthropods in a completely artificial fashion. Clearly, the ability to detoxify secondary metabolites of mushrooms is widespread throughout taxa of arthropods. This ability obviously has evolved more than once among families of Diptera. Furthermore, groups of basidiomycete taxa (e.g., *Amanita* spp., *Galerina* Earle spp.) considered deadly to most animals, including non-mycophagous Diptera, have no detrimental effect on mycophagous species (Jaenike et al. 1983, Jaenike 1985).

Mycophagous Diptera may be of some benefit to their fungal host. Stinkhorns (Phallales: Basidiomycotina) benefit from scavenging flies that disperse their basidiospores. Hodge et al. (1997) discussed the carriage of fungal material by adult *Drosophila*. Ascomycete fungi (including members of the genus *Balansia*) are known to benefit from symbiotic associations with insects. Recently, Diptera have been shown to disperse spermatia (a type of fungal spore) from one fungus to other individuals, thus facilitating fertilization (a sort of "pollination") (Bultman et al. 1998, 2000).

Clearly, this study indicates a great need for additional investigations into the interrelationships between fungal host and mycophagous Diptera. Likewise, there are many uncertainties regarding the life histories for many species of mycophagous flies, as well as the interrelationships among the mycophagous Diptera.

Acknowledgments

Sincere thanks are given to Dr. Benjamin Foote for identification of dipteran material and for critical review of this manuscript. Thanks also are extended to Dr. Tom Bruns and two anonymous reviewers for their helpful comments. This work was supported in part by a grant from the Geauga County (Ohio) Park District.

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